



A review of tef physiology for developing a tef crop model

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ABSTRACT

Tef (*Eragrostis tef* (Zucc.) Trotter) is important for Ethiopian food security and a significant source of income for smallholder farmers in Ethiopia. In industrialized nations, tef is becoming a popular health food due to its lack of gluten and high nutritional value. Though tef is an important crop within Ethiopia, research on the crop has been limited. Crop models are an important tool for assessing food security, the effectiveness of management practices, and the impacts of climate change on crop production. The only existing crop models for tef are the FAO-AEZ crop growth simulation model, and the FAO AquaCrop model, which focuses on water limited crop production. The FAO AEZ model only produces final yields, which limits its applicability. The AquaCrop model has been validated using data from northern Ethiopia under current climate conditions without nitrogen limitations. As tef production spreads across the world, and Ethiopia suffers from soil fertility depletion and climate change, there is a need for a more comprehensive tef model. Tef, a short-day C4 crop, shows a high level of genetic diversity, resulting in large variation in water use, water use efficiency, growing season length, and even photosynthetic rate across cultivars. Tef quickly reaches a closed canopy, resulting in a higher early-season water use efficiency than wheat (C3 crop) or sorghum (C4 crop). Lodging is a significant yield limitation in tef, and is often exacerbated by fertilizer applications. There are several areas of tef research that have limited, or no, published data, especially on a field level, which will hinder future tef model development. These areas include the effects of temperature on photosynthesis and phenology, the effects of heat stress on senescence, the effects of elevated atmospheric CO₂ on photosynthesis and transpiration, and a field level lodging model. By combining relevant information from other crops with the available tef literature, however, it should be possible to create a tef crop model prototype.

1. Introduction

Tef, also known as *teff*, *t'ef*, *Lovegrass*, *Annual Bunch Grass Teff*, *Warm Season Annual Bunch Grass*, *Williams Lovegrass*, *Abyssinian Lovegrass*, or by its scientific name *Eragrostis tef* (Zucc.) Trotter, is an ancient Ethiopian staple grain (Araya et al., 2011; Miller, 2011). Tef flour is the preferred ingredient to make the traditional Ethiopian flatbread *enjera*, and the grain is also used to make porridge and some varieties of local alcoholic beverages (Van Delden, 2011). Tef is considered to be a highly nutritious grain, with a slightly higher protein content than sorghum or maize (NRC, 1996), balanced amino acids, and a high lysine content (Jansen et al., 1962). Tef has a high iron content (Mengesha, 1966; Costanza et al., 1979), though study results on this have varied (Besrat et al., 1980), and a significantly higher calcium content than most major grains (Vohwinkel et al., 2002). Tef is also gluten free (Spaenij-Dekking et al., 2005), which has resulted in a growing demand for tef in industrialized nations. This emerging market has led to efforts to introduce tef grain production in industrialized

nations.

Around the world, tef is most widely known as a forage crop. It was introduced as a forage crop to countries such as Australia, India, Kenya and South Africa as early as the end of the 19th century (Costanza et al., 1979) and spread to many other parts of the former British Empire (Van Delden, 2011). Today, tef is gaining popularity as a low input hay crop in the USA (Curtis et al., 2008), with an estimated 100,000 ha under tef forage production in 2010 (Miller, 2011). Improved forage varieties, which mature more slowly to allow for longer vegetative growth, have been bred in the USA and are commercially available (Boe et al., 1986; Miller, 2008). Unlike most warm season forage crops, tef produces both a high quantity and quality of forage during the hot summer months (Boe et al., 1986) and is not prone to nitrate toxicity, which makes it useful for overcoming summer forage shortages (Miller, 2011). Apart from forage production, tef is also used as a green manure and as an erosion control crop in the USA (Miller, 2011).

While there is some production of tef for grain in the United States, Canada, Australia, and the Netherlands (Eckhoff et al., 1997; Seyfu,

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1997; Van Delden, 2011) the vast majority of tef grain production is still in Ethiopia. The strong preference of Ethiopian consumers for tef over other grains means that farmers can demand higher prices for tef grain (Seyfu, 1997). Tef straw also brings in a higher price than other types of straw, as it is a superior feed and is also used for construction purposes (Seyfu, 1997; Van Delden, 2011). Apart from tef being a cash and a food crop, Ethiopian farmers prefer planting tef for several reasons. Tef is considered to be more tolerant of waterlogging than other cereals (Seyfu, 1997). Waterlogging is an especially common problem for Vertisol soils, which account for 23% of the total area under cultivation in Ethiopia (Getu, 2012). At the same time, tef is also seen as more tolerant of drought stress than other grains (Seyfu, 1997). Takele (2001) noted, that as drought becomes more prevalent in the semi-arid regions of Ethiopia, more farmers are shifting away from maize and sorghum production, and towards tef, as this fast growing crop is more likely to mature before the onset of the dry season. Tef is also less susceptible to diseases than other grains (Stewart and Dagnachew, 1967), and is not prone to post-harvest losses due to weevils and other storage pests (Seyfu, 1997).

Tef is a self-pollinating (Melak, 1964; Berhe and Miller, 1976), panicle bearing, annual, C4 crop (Kebede et al., 1989). Fig. 1 illustrates the tef panicle in detail. Tef seeds are small, with a typical 1000-seed weight of only 265 mg (Seyfu, 1997). Each plant has multiple tillers, though the number of tillers depends on the cultivar and nutrient availability (van Delden et al., 2010; Giday, 2012). Ali (2013) also found that the number of tillers decreased under lower soil water contents or higher air temperatures. The number of tillers per plant varies from as low as 2 (Ali, 2013) to as high as 22 tillers per plant (Giday, 2012). The average plant height for tef is about 1 m (Seyfu,

1993), but plant heights from 31 to 155 cm have been measured (Seyfu, 1993), with cultivar genetics and growing conditions being the major sources of variation (Seyfu, 1993; Ali, 2013). The time to maturity ranges from 60 days (Seyfu, 1997) to 150 days (Getu, 2012) depending on growing conditions and the cultivar.

Crop models are used to simulate the growth and yields of crops under varying environmental and management conditions (Asseng, 2004). Crop models are important tools for understanding the impact of climate change on yields and for evaluating food security (Asseng et al., 2011). Crop models also provide a valuable resource for virtually testing crop traits. Unlike field experiments, which are time consuming and expensive, computer based crop models are fast and inexpensive enough to run hundreds of growing scenarios (Asseng, 2004). Fig. 2 shows a basic schematic of a crop model. Historically, most crop models were developed for global staple crops, such as wheat, but there are many crops, such as tef, which are important to food security on a local scale, even if they are not well known globally (Araya et al., 2010).

Climate change could significantly affect Ethiopian crop production. Mean maximum temperatures are expected to rise by 2.2–2.7 °C by 2050 in northern Ethiopia (Hadgu et al., 2015). Mean minimum temperatures are expected to rise by 1.4–1.7 °C by 2050 (Hadgu et al., 2015). The frequency of hot days and nights is also expected to increase (Hadgu et al., 2015). Increasing temperatures could cause heat stress and an increase in evapotranspiration (Niang et al., 2014). While the total annual rainfall is expected to increase, it is uncertain what effects climate change will have on rainfall distribution, timing, and intensity (Hadgu et al., 2015). Since Ethiopian agriculture is mostly rainfed (Habtegebrial et al., 2007; McHugh et al., 2007), increased water losses through evapotranspiration and more erratic rainfall could have serious

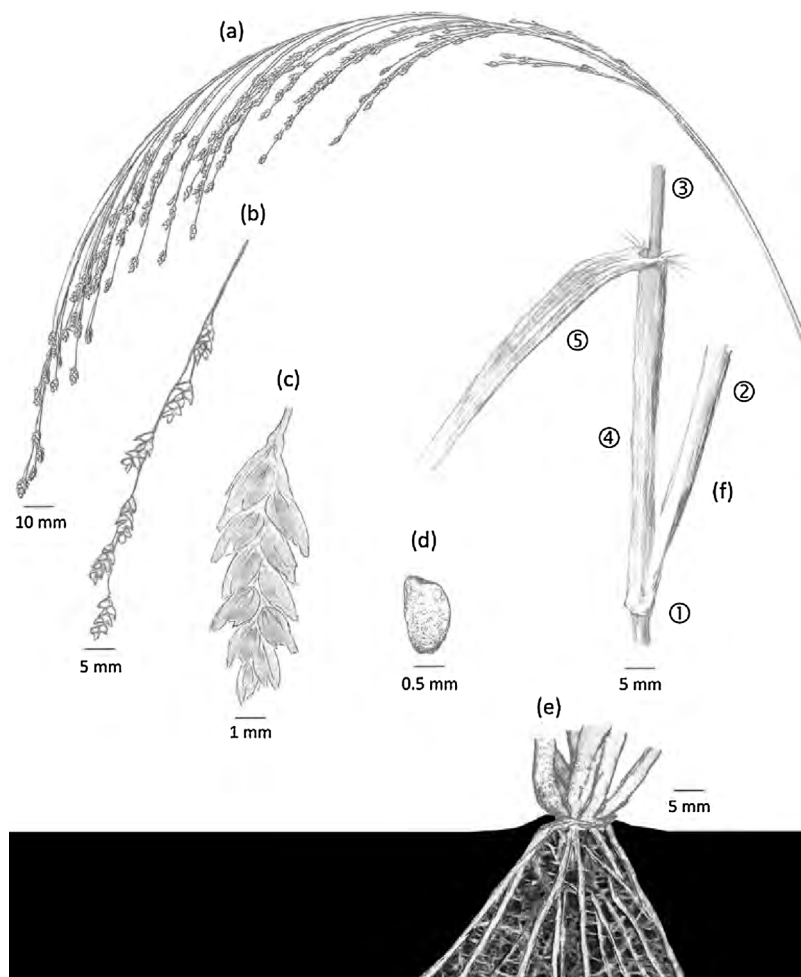


Fig. 1. Drawing of (a) ripening inflorescence of tef (drooping panicle); (b) branch of the panicle, containing spikelets; (c) individual spikelet, containing tef grains; (d) individual tef grain; (e) tef stubble and root system; (f) tef phytomer: (1) node, (2) axillary branch, (3) internode, (4) leaf sheath and (5) leaf blade (Van Delden, 2011).

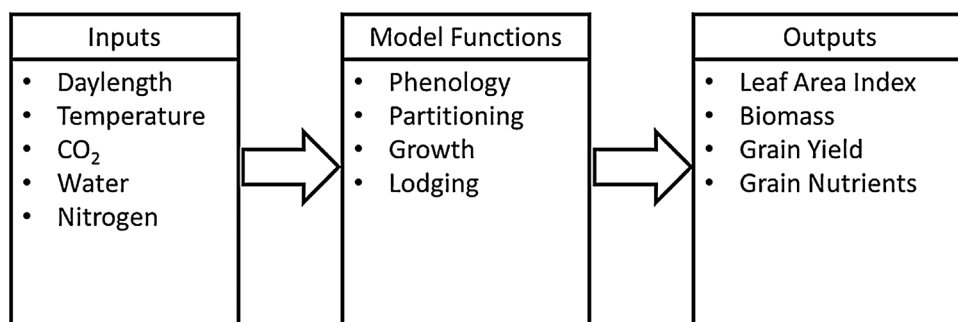


Fig. 2. A schematic of the basic inputs, functions, and outputs of a crop model.

repercussions for food security. A tef crop model would allow researchers to quantify the effects of climate change on tef production. In turn this information could be used to develop strategies to minimize yield losses, or to improve the response to threats to food security.

The goal of this paper is to review the available research on tef physiology needed to develop a crop model for tef. The physiology and modeling approaches for sorghum are also examined in order to provide context and to fill in gaps in the data. The paper covers seven major topics: a review of existing tef models, phenology, growth, water and nitrogen effects, crop management, lodging, and field data availability. The publications reviewed for this paper were collected using Web of Science, Google Scholar, and the digital libraries of tef researchers, which provided the authors access to publications that are not readily available online.

2. Existing tef crop models

There are currently only two published crop models for tef, the Food and Agriculture Organization (FAO)-AEZ crop growth simulation model (Yizengaw and Verheye, 1994), and the FAO AquaCrop model (Araya et al., 2010). The FAO-AEZ model uses three steps to estimate yields. The first step is to calculate radiation limited yield, the second is to estimate water limited yield, and the third step is to add soil and management limitations (Yizengaw and Verheye, 1994). Each step is calculated based on the results of the previous step. As the length of the crop growth cycle is an input, the model cannot model changes in phenology in response to temperature or day length (Yizengaw and Verheye, 1994). This model only produces final yields, which limits its applications (Yizengaw and Verheye, 1994). AquaCrop uses daily crop transpiration and normalized crop water productivity (NCWP) to estimate biomass production (Araya et al., 2010). NCWP is calculated by dividing the biomass yield by the sum of the dividend of transpiration and reference evapotranspiration (Araya et al., 2010). Grain yield is calculated using the biomass yield and a crop specific harvest index (Steduto et al., 2009). Unlike most crop models, AquaCrop directly models percent canopy ground cover, rather than calculating it based on the modeled leaf area index, or LAI (Steduto et al., 2009). As AquaCrop does not simulate LAI, its methods for calculating transpiration and for splitting evapotranspiration into evaporation and transpiration differ from other crop models (Steduto et al., 2009). Crop specific parameters, such as leaf expansion growth, canopy development, and canopy senescence are used to model the canopy ground cover (Steduto et al., 2009). The model also calculates the available soil water by balancing the soil water inputs from rainfall and irrigation with the outputs, such as runoff, evaporation, transpiration, and deep percolation (Araya et al., 2010). Factors ranging from 0 to 1 are used to describe the effects of water stress on stomatal conductance, canopy senescence, and leaf growth (Araya et al., 2010).

The AquaCrop tef model was developed and calibrated using field data sets from northern Ethiopia (Araya et al., 2010; Araya et al., 2011; Tsegay et al., 2012; Tsegay et al., 2015; Haileselassie et al., 2016). The model has not been tested for environmental conditions outside of

Ethiopia. None of the studies used for calibrating the AquaCrop model examined the effects of elevated atmospheric CO₂, daylength, lodging, or extreme temperatures (Araya et al., 2010; Araya et al., 2011; Tsegay et al., 2012; Tsegay et al., 2015; Haileselassie et al., 2016). While the AquaCrop model performed well under water limited scenarios with current temperatures and atmospheric CO₂ levels in northern Ethiopia, it is unknown how effective it would be under future climate scenarios, or at higher latitudes. The AquaCrop model also does not take nutrients, such as nitrogen, directly into account (Araya et al., 2010), so it cannot model nutrient limited scenarios. Ethiopian soils, however, are degraded (Haileselassie et al., 2005) and the use of fertilizer inputs is not widely practiced by farmers (Getu, 2012). Therefore, it is crucial to develop a crop model for tef, that also accounts for nutrients, in particular nitrogen.

3. Phenology

3.1. Introduction

Phenology controls the life cycle of a plant (Asseng, 2004). It is affected by temperature, and in some crops phenology is also regulated by day length. Accurately simulating phenology is critical to creating a successful model, as phenology regulates carbon partitioning, leaf development, and ultimately yield.

3.2. Germination

Tef requires a minimum temperature of 10 °C to germinate (Van Delden, 2011). Miller (2011) recommended delaying planting until soil temperatures reach 18 °C or higher. Seed germination experiments for tef appear to be focused on factors such as temperature and seed treatment, rather than soil moisture (Ghebrehewot et al., 2008; Evert et al., 2009). According to Seyfu (1993), the time between sowing and germination can vary from 4 to 12 days, with a mean of 5 days. Ghebrehewot et al. (2008) found, however, that after 16 days, the percent of germinated seeds varied between 40.7% and 75.8% depending on the temperature and length of day light. This experiment was done in a lab and designed to look at the effectiveness of seed treatments on altering germination, and used 16 days as a standard time of measurement, so it might not be a reliable maximum time between sowing and germination.

3.3. Emergence

The number of days until emergence reported in studies ranged from 5 days (Araya et al., 2010) to 14 days, though this particular study measured the number of days until 90% emergence (Evert et al., 2009). Norberg et al. (2009) reported that emergence occurs within 3–7 days, when the mean soil temperature of the top 10 cm is 16 °C or higher. Evert et al. (2009) found that warmer temperatures sped up the rate of emergence, but that by 9 days after planting, the number of emerged plants was the same across all four temperature treatments. The

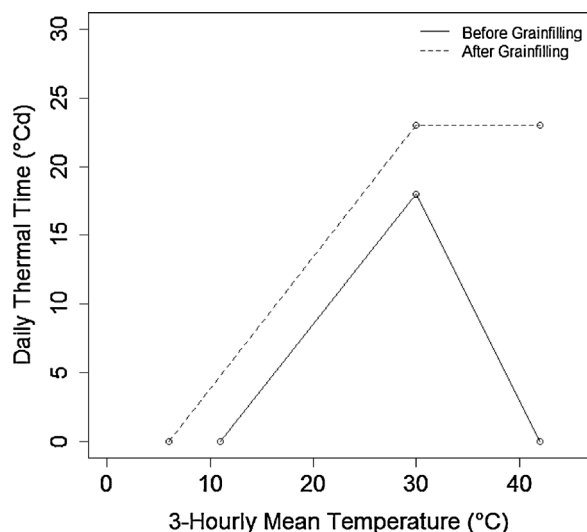


Fig. 3. The effect of three-hourly mean temperature on daily thermal time for phenology. The day is split into eight, three hour long blocks. The temperature for each of these eight blocks is interpolated from the daily maximum and minimum air temperatures. Thermal time is estimated for each of the eight blocks and is then averaged to create the daily thermal time. Different rates of thermal time accumulation are used for before and after grain filling (Keating et al., 2003).

recommended planting depth for tef varies from source to source, though a shallow depth is recommended. Norberg et al. (2009) recommend a planting depth between 3 and 6 mm. Aberra (1992) found that a planting depth between 5 and 15 mm had no negative effect on germination or plant height, but that a planting depth of 0 mm or greater than 15 mm had a negative effect on plant height, and that a planting depth of 0 mm or greater than 20 mm also had a negative effect on germination. Van Delden (2011) recommended a maximum planting depth of 10 mm. Evert et al. (2009) found that the initial rate of emergence was highest at planting depths between 6 and 13 mm, but there was no emergence at a planting depth of 50 mm.

There is little information available on the effects of soil moisture on emergence. Norberg et al. (2009) simply stated that the soil moisture had to be adequate for rapid emergence, but did not define 'adequate'. The only report found of a study involving the effect of soil moisture on seed emergence for tef was a reference to unpublished data from Abuhay, which indicated that there was significant variation in percent seedling emergence among tef cultivars under soil moisture deficit conditions (Takele et al., 2001). Decreasing soil moisture from 85% to 25% field capacity decreased the percent emergence for all cultivars, though of the cultivars tested, the variety DZ-Cr-37 had the highest percentage of emergence for all soil moisture treatments (Takele et al., 2001).

3.4. Heading

Tef is a short day plant (Van Delden, 2011). Seyfu (1997) noted that tef performs best when the day length is approximately 12 h. In Ethiopia, the day length during the main growing season varies between 13 h at planting and 10 h at harvest (Van Delden, 2011). The time to heading has been found to significantly increase when the plant is exposed to long periods of daylight, which has made it difficult to grow tef at higher latitudes (Seyfu, 1983; Van Delden, 2011). There is also a difference in time until heading between cultivars (Teklu and Tefera, 2005; Van Delden, 2011). Van Delden (2011) found that the native Ethiopian cultivars Gibe, also spelled Ghibe, and Ziquala had their time until heading increased by 129% and 140% respectively, when the day length was increased from 9 to 18 h. Teklu and Tefera (2005) reported the times until heading for the Gibe and Ziquala cultivars were 39 and 35 days respectively, when they were grown in a

field experiment in Ethiopia. The same cultivars grown in a greenhouse in the Netherlands varied in days until heading from 31 days to 72 days and 39 days to 94 days respectively depending on whether the day length was 9 or 18 h (Van Delden, 2011). The cultivars Ayana and 04T19, which have been bred for Dutch production, however, only had increases in time to heading of 29% and 60% respectively when the day length was increased from 9 to 18 h (Van Delden, 2011). Critical day length is the day length above which the time to heading is affected. Van Delden (2011) reported that critical day length for tef varies across cultivars and that it differs between the main stem and the third tiller. The average critical day lengths for the various cultivars were 11.4 h for Gibe, 12.0 h for Ziquala, 10.8 h for Ayana, and 11.1 h for 04T19 (Van Delden, 2011).

Both Getu (2012) and Giday (2012) found that the amount of fertilizer applied also influenced the days until heading, although the mechanism for this is not clear. Getu (2012) found that increasing the amount of nitrogen fertilizer from 0 kg N/ha to 69 kg N/ha increased the days to heading from 69 to 81. Giday (2012) found that the same change in fertilizer input increased the number of days until 50% heading from 56 to 62. It has been suggested that the shorter time until heading under lower input systems is a limitation avoidance response in which the plant develops rapidly in order to reproduce before the limited soil nutrients run out (Giday, 2012).

3.5. Temperature effect on phenology

The base temperature for tef has been reported to be 7.8 °C (Van Delden, 2011) and 7 °C (Haileselassie et al., 2016). This is lower than the 11 °C base temperature of pre-grain filling sorghum (Keating et al., 2003). Seyfu (1997) reported that tef grew best in a temperature range from 10 °C to 27 °C Teshome and Verheye (1993), however, wrote that the optimum temperature range was 15–21 °C. Miller (2011) reported that optimum yields were achieved when the growing temperature was 26 °C or higher. It is unclear where exactly in these ranges the temperature for maximum phenological thermal time accumulation falls. As factors such as improved photosynthesis, water use, and nitrogen availability can affect optimal yield, it is possible that there is a disconnect between phenological studies and productivity studies. Tef does not have a vernalization requirement (Van Delden, 2011), and in fact cannot tolerate freezing temperatures at any stage of development (Norberg et al., 2009). Tsegay (2012) reported that the upper limit of tef's temperature tolerance is 35 °C.

Fig. 3 shows the approach taken by the APSIM sorghum model to simulate the effects of temperature on daily thermal time accumulation. Lobell et al. (2012) studied satellite data of wheat fields under high temperatures in India and found that the time of grain filling decreased under high temperatures, leading to earlier senescence. Parent et al. (2010) also found that traditional linear thermal time models were not representative of crop behavior under extreme temperatures. The APSIM sorghum model addresses the concerns raised by Lobell et al. (2012) by having the post-grain filling part of the model plateau at extreme temperatures, rather than go to zero (Keating et al., 2003).

While the research on the effects of temperature in general, and extreme temperatures in particular, on tef phenology is limited, it is likely that tef would act similarly to sorghum, another C4 crop. Therefore, any tef model would have to take accelerated senescence under extreme temperatures into account. Having two separate thermal time accumulation functions for before and after grain filling could accomplish this. There is no reported temperature for maximum daily thermal time accumulation for tef. The optimal growing temperature ranges given by Seyfu (1997), Teshome and Verheye (1993), and Miller (2011) suggest that the temperature for maximum daily thermal time accumulation lies at or below 26 °C. As a C4 crop, however, it would be expected for tef to have a temperature response closer to that of sorghum, which is modeled with a thermal time accumulation peak at 30 °C in the APSIM-Sorghum model (Keating et al., 2003).

Table 1
1000-grain weights of tef.

1000 Grain Weight (g)	Notes	Source
0.25–0.5		(Van Delden, 2011)
0.25–0.35	Variation due to different fertilizer treatments	(Giday, 2012)
0.277–0.419	Note, the values are reported as being in mg/100-grains, but should be in g/1000-grains. The range is due to varying cultivars.	(Teklu and Tefera, 2005)
0.265		(Seyfu, 1997)
0.236–0.286	The range is due to varying cultivars.	(Vohwinkel et al., 2002)
0.0947–0.309	The range is due to varying seed size and planting depth.	(Bedada, 2009)

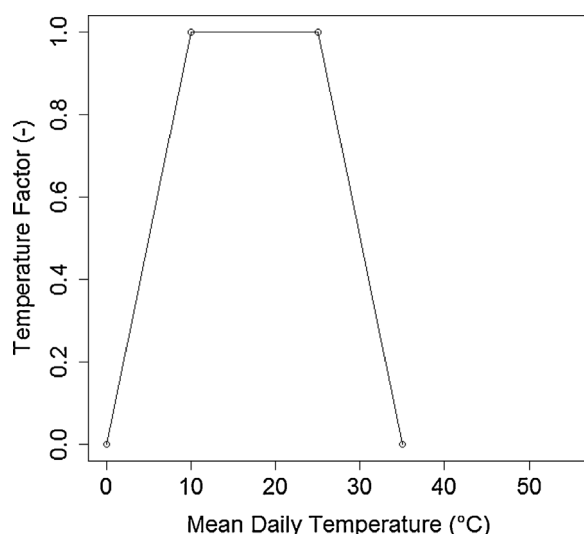


Fig. 4. The effect of the weighted daily temperature ($0.25 \times T_{\min} + 0.75 \times T_{\max}$) on RUE in CERES-Sorghum (White et al., 2005).

4. Growth

4.1. Initial conditions at emergence

The tef AquaCrop model sets the canopy cover per seedling, at 90% emergence, as 1.5 cm^2 (Araya et al., 2010). The shoot biomass of tef as a seedling varies depending the size of the seed and the sowing depth (Bedada, 2009). Measurements of the shoot biomass for seedlings varied from 0.00166 g/plant to 0.00313 g/plant , with a mean of 0.00238 g/plant (Bedada, 2009). The exact carbohydrate reserve of tef seeds at emergence is unknown. Tef seed is reported to be 73% carbohydrate (Bultosa and Taylor, 2004). Table 1 shows the reported 1000-grain weights for tef from various papers. As noted in Table 1, it is likely that Teklu and Tefera (2005) reported the 1000-grain weight in g, rather than the 100-grain weight in mg. All of the other reported values (Seyfu, 1997; Vohwinkel et al., 2002; Bedada, 2009; Giday, 2012) fell within the range given by Van Delden (2011), so that the carbohydrate reserve of a tef seed can be calculated as being between 0.000183 and 0.000365 g .

4.2. Temperature effects on growth

Models often use radiation use efficiency (RUE) to simulate photosynthesis (White et al., 2005; Zheng et al., 2014). The light extinction coefficient (k) is used to describe the transmission of radiation to leaves lower in the canopy. A high k value indicates a crop that intercepts most of the radiation at the top of the canopy, with little radiation penetrating deeper into the canopy (Bingham and Topp, 2009). There is no known RUE or k for tef. Kebede et al. (1989), however, measured the carbon exchange rate (CER) of tef under varying temperature and light conditions. The CER of tef, at a photosynthetic photon flux rate (PPFR) of $1800 \mu\text{mol}/\text{m}^2/\text{s}$, was highest at temperatures between 36

and 42°C , with an average CER of $27 \mu\text{mol}/\text{m}^2/\text{s}$ (Kebede et al., 1989). The highest CER measured was $31.8 \mu\text{mol}/\text{m}^2/\text{s}$, which occurred at a temperature of 35°C and a PPFR of $2000 \mu\text{mol}/\text{m}^2/\text{s}$ (Kebede et al., 1989). Ali (2013) noted that photosynthetic CO_2 assimilation ($\mu\text{mol CO}_2/\text{m}^2/\text{s}$) and stomatal conductance of water vapor ($\text{mol H}_2\text{O}/\text{m}^2/\text{s}$) decreased with increasing temperature and increasing day length. Maximum photosynthetic CO_2 assimilation, which was $16 \mu\text{mol CO}_2/\text{m}^2/\text{s}$, occurred under a maximum daily temperature of 24°C and a minimum daily temperature of 19°C . The two higher temperature treatments ($T_{\max} = 27$ and 30 and $T_{\min} = 16$ and 24°C) resulted in lower photosynthetic CO_2 assimilation (Ali, 2013).

Kebede et al. (1989) found a significant difference in CER between the two cultivars tested, especially at the extreme ends of the temperature spectrum. It was noted that the Red Dabi cultivar, which had a higher CER than the DZ-01-354 variety, is an early maturing variety that was bred for the warmer parts of Ethiopia (Kebede et al., 1989). It is possible that this adaptation to warmer climates also resulted in higher CER at high temperatures, but it is unclear how this would have resulted in the 28.6% difference in CER at the lowest temperature, 18°C .

Models generally represent the effect of temperature on photosynthesis, by multiplying RUE with a unitless temperature factor that varies between 0 and 1 depending on the temperature (White et al., 2005; Zheng et al., 2014). The function for the temperature factor has a trapezoidal shape (see Fig. 4). Sorghum performs better at higher temperatures, with an optimum range between 20 and 40°C (White et al., 2005). The research performed by Kebede et al. (1989) suggests that the optimal range for tef is between 36 and 42°C , though since the temperature step for this experiment was 6°C , the range could be larger. There were no measurements for temperatures below 18°C , so the minimum temperature is unknown. It is likely that tef, like sorghum, would have a photosynthetic base temperature above 0°C . The phenological base temperature of 7.8°C (Van Delden, 2011) could serve as a reasonable estimate for a tef model, until further research is performed. As stated earlier, there appears to be a significant difference in temperature response between tef cultivars at high temperatures (Kebede et al., 1989). As only two cultivars were used for this study, it is difficult to conclude how widespread this difference is, but the available evidence suggests that particularly the maximum photosynthetic temperature could vary between cultivars. This would require special attention when creating a tef model, as crop models normally treat the photosynthetic-temperature range as constant throughout a crop species.

4.3. Carbon partitioning

There are no published measurements of stem partitioning for tef. A study of tef for feed purposes measured the botanical fractions of tef straw across multiple cultivars. The parts of the plant measured were the stem, leaves, panicle, and chaff. The measurements were given as $\text{g}/100 \text{ g}$. The stem fraction ranged from 37 to $46 \text{ g}/100 \text{ g}$, with a mean of $42 \text{ g}/100 \text{ g}$ (Bediye et al., 1996). Therefore, the best estimate currently available for the stem partitioning fraction is 0.42 . The available data on leaf area for tef, focuses on leaf area per plant, or flag leaf area, not

leaf area index (Tekalign, 2007; Ali, 2013). As these experiments did not record plant density at the time of leaf area measurement, it is impossible to scale up the plant level measurements to a unit area based measurement.

4.4. Root growth

For well-watered conditions, Degu et al. (2008) found significant variation in the total root length, with values ranging from 536 to 4179 cm under well irrigated conditions depending on the cultivar. Ayele et al. (2001) did not publish a root length value, but they did measure root depth and weight. Values for root depth under well irrigated conditions ranged from 86 to 116 cm depending on the cultivar (Ayele et al., 2001). Under drought conditions, the root depth varied from 59 to 100 cm and the root weight varied from 0.42 g to 1.29 g per plant depending on the cultivar (Ayele et al., 2001). Cultivars with thicker roots were found to have deeper roots (Ayele et al., 2001). While root depths reached over a meter, the majority of the root biomass was found in the top 30 cm of the soil (Ayele et al., 2001). Ayele et al. (2001) also found a significant correlation between the plant height and the root depth.

4.5. CO₂ effects

There are no known studies of the effects of elevated CO₂ on tef. As tef is a C4 plant (Kebede et al., 1989), however, it can be assumed that higher CO₂ levels would have little effect on its photosynthetic efficiency. Millet or sorghum models could be used as a basis for approximating the effects of elevated CO₂ on tef as these are both C4 crops. The water use efficiency (biomass production/total evapotranspiration) of sorghum increased by 28% when atmospheric CO₂ levels were elevated by 200 ppm, which corresponds to a 14% increase per 100 ppm CO₂ above 370 μmol CO₂/mol (Triggs et al., 2004). The leaf photosynthetic rate for sorghum was found to increase by 9% when the atmospheric CO₂ was raised from 350 to 700 μmol CO₂/mol, which resulted in a 2.6% increase per 100 ppm CO₂ above 350 μmol CO₂/mol (Prasad et al., 2006).

5. Water and nitrogen effects

5.1. Evapotranspiration

The most thorough research available on evapotranspiration in tef is from the research surrounding the AquaCrop tef model (Araya et al., 2010; Araya et al., 2011; Tsegay et al., 2012). The crop coefficient (Kc) is a crop specific factor used to convert reference evapotranspiration (ET_o) to crop evapotranspiration (ET_{crop}) (Doorenbos and Pruitt, 1977). Table 2 shows that tef has a much higher initial Kc than wheat or

Table 2
Crop coefficient (kc) for tef (Araya et al., 2011), sorghum, and wheat (Brouwer and Heibloem, 1986).

	Tef	Sorghum	Wheat
Initial ^a	0.8–1.0	0.35	0.35
Vegetative ^b	0.95–1.0	0.75	0.75
Mid ^c	0.95–1.1	1.10	1.15
Late ^d	0.4–0.5	0.65	0.45

^a The timing for this stage is 14–16 days after planting (DAP) for tef (Araya et al., 2011), 20 DAP for sorghum, and 15 DAP for wheat (Brouwer and Heibloem, 1986).

^b The timing for this stage is 32–37 DAP for tef (Araya et al., 2011), 50–55 DAP for sorghum, and 40–45 DAP for wheat (Brouwer and Heibloem, 1986).

^c The timing for this stage is 65–72 DAP for tef (Araya et al., 2011), 90–100 DAP for sorghum, and 90–110 DAP for wheat (Brouwer and Heibloem, 1986).

^d The timing for this stage is 77–88 DAP for tef (Araya et al., 2011), 120–130 DAP for sorghum, and 120–150 DAP for wheat (Brouwer and Heibloem, 1986).

sorghum. This is because tef has a large tillering rate and quickly achieves a closed canopy, which results in minimal evaporative losses (Tsegay et al., 2012) and more effective radiation interception. The Kc value for tef is slightly lower than that for wheat in the mid growth stage, but roughly the same as the sorghum Kc at the same stage. Late in the season, sorghum has a higher Kc than tef, but the Kc of tef and wheat are roughly the same. The growing season for tef is much shorter than that of wheat or sorghum (Brouwer and Heibloem, 1986; Araya et al., 2011). The short growing season could account for the higher initial Kc, as tef grows faster than wheat or sorghum. The tef cultivars used in the experiment shown in Table 2 were early maturing varieties (Araya et al., 2011), which means that the values given for growth phase durations are not accurate for all tef varieties. It is possible that the initial and vegetative Kc values of late maturing tef varieties are closer to those of wheat or sorghum. Another factor to consider is that ET_o and as a result Kc, can vary depending on the reference crop used (Fangmeier et al., 2006), the relative humidity, and the windspeed (Brouwer and Heibloem, 1986). Brouwer and Heibloem (1986) suggested a variation of 0.1 for their reported Kc values depending on the relative humidity and wind speed. The crops in question were grown under different weather conditions, so this variation could account for some the differences in Kc between tef, wheat, and sorghum in the mid to late growing stages.

5.2. Water use efficiency

There is limited published information available on the water use efficiency of tef. The AquaCrop model uses the normalized crop water productivity (NCWP), which is the biomass yield divided by the cumulative ratio of transpiration normalized for climate (Araya et al., 2010). Tsegay et al. (2012) approximated the cumulative ratio of transpiration normalized for climate by taking the cumulative ratio of actual evapotranspiration (ET_a) over reference evapotranspiration (ET_o) ($\Sigma(ET_a/ET_o)$) (Tsegay et al., 2012). Tsegay et al. (2012) assumed that actual evapotranspiration was equivalent to the simulated transpiration, as the tef canopy closed early in the season resulting in minor evaporative losses. The approximated normalized crop water productivity (WP*) was the slope of the linear regression curve between $\Sigma(ET_a/ET_o)$ and the corresponding biomass yield (Steduto et al., 2007). The WP* values used in AquaCrop were 14 g/m² for local tef varieties and 21 g/m² for improved varieties (Tsegay et al., 2012). The varieties used were of intermediate growing season length, so it is unclear if the WP* values would be the same for faster or slower maturing varieties (Tsegay et al., 2012).

Tef has been found to have a lower normalized crop water productivity than other C4 crops (Araya et al., 2010; Tsegay et al., 2012). The WP* value used for maize in AquaCrop is 33.7 g/m² (Hsiao et al., 2009). For sorghum, AquaCrop uses a WP* of 32.9 g/m² (Steduto and Albrizio, 2005). Araya et al. (2010) suggested this could be caused by N limitations and a short growing season. N limitations during the experiment could have been the result of leaching or denitrification (Araya et al., 2010). The recommended rate of N fertilizer for tef is also lower than that of other C4 crops, as tef becomes highly susceptible to lodging under higher fertilizer rates (Habtegebrial et al., 2007). Tsegay et al. (2012) proposed that the lower WP* could be caused by tef's higher than average for C4 crops grain protein content, which would require more energy per unit dry weight to convert assimilated CO₂ into plant matter. Tef's low light use efficiency was also suggested as an explanation (Tsegay et al., 2012).

Another study found that grain water use efficiency (WUE), which is the ratio of grain yield to total transpiration, increased with increasing supplemental irrigation, as seen in Table 3 (Araya et al., 2010). The increase in yield plateaued at about 100 mm of supplemental irrigation, which combined with the rainfall of the location provided 90% of the optimal water requirement (Araya et al., 2011). The biomass WUE, which is the ratio of biomass yield to total transpiration, however,

Table 3

Water supply, transpiration, and grain and biomass water use efficiency for tef across multiple locations and irrigation treatments (Araya et al., 2010).

Site (Year)	Water Supply (mm)	Transpiration (mm/ha) ^a	BM-WUE (kg/mm) ^b	Grain-WUE (kg/mm) ^b	HI ^b
Mekelle (2008)	280	140	27.3	13.9	0.26
	256	119	24.3	9.9	0.19
	232	99	23.3	9.8	0.18
	205	76	22.6	9.6	0.16
	185	66	21.3	9.7	0.16
Ilala (2008)	188	69	19.7	5.1	0.09
	367	128	15.8	10.9	0.24
Mekelle (2009)	318	95	14.3	6.5	0.13
	278	70	12.5	5.3	0.11

^a As determined by the AquaCrop model (Araya et al., 2010).

^b BM = final measured aboveground biomass, WUE = water use efficiency (kg dry matter/mm transpiration), and HI = Harvest Index.

increased with decreasing supplemental irrigation, implying that deficit irrigation would be beneficial for tef straw production (Araya et al., 2010). Green WUE, which is 100 times the sum of transpiration divided by the seasonal precipitation and irrigation from planting to maturity, appeared to increase with an increase in water supply (Araya et al., 2010). Differences in harvest index, the ratio of grain yield to biomass yield, and WUE between the two experiments at the Mekelle site in Table 3 were due to two different cultivars being used. In 2008, an improved cultivar called DZ-974 was used, while in 2009 a local variety called Keyh was planted (Araya et al., 2010). Another possible cause for variation in WUE is the difference in weather, and in particular vapor pressure difference, between the two years, which would influence transpiration. Grain WUE for wheat ranges from 4.8 to 20.0 kg/ha mm (French and Schultz, 1984), which is higher than the grain WUE range for tef (Araya et al., 2010). The biomass WUE of wheat ranges from 17.5 to 55.0 kg/ha mm (French and Schultz, 1984), which is higher than the range reported for tef (Araya et al., 2010).

5.3. Water stress responses

Tef grain yields have a moderate response to drought stress, but yields are particularly sensitive to water stress during the early establishment and flowering stages (Mengistu, 2009; Araya et al., 2011). Reported yield reductions due to drought stress under field conditions ranged from 14% (Belay and Baker, 1996) to 77% (Takele, 2001) when the drought stress occurred at anthesis. Takele (2001) attributed these yield losses to reduced relocation from vegetative sources to the grain sinks. Water stress early in the growing season was found to increase the time to heading and maturity, while water stress late in the growing season was found decrease the time until maturity (Teferra et al., 2000).

Osmotic adjustment (OA) is the net rise in solutes within the plant cells in response to water stress (Morgan, 1984). There is a significant variation in OA among tef cultivars (Ayele et al., 2001; Takele et al., 2001; Degu et al., 2008), with measured values ranging from 0.12 MPa to 1.38 MPa depending on the cultivar and the drought severity (Degu et al., 2008). The interaction of environment and genotype can have a significant impact on OA in tef, but the extreme OA varieties, both on the low and the high end, were found to have consistent OA values across multiple growing seasons (Ayele et al., 2001). Cultivars with a higher OA tend to last longer under stress conditions as they are better at maintaining a high relative water content than cultivars with a low OA (Ayele et al., 2001; Takele et al., 2001). While cultivars with a higher OA showed a higher rate of survival during stress, they did not have a higher increase in shoot dry weight per day during this time than

the low OA cultivars (Ayele et al., 2001; Takele et al., 2001). This focus on survival, rather than productivity, is more typical in wild plants than domesticated ones (Ayele et al., 2001). Degu et al. (2008) found that the relative growth rate (RGR) of the shoot dry weight varied between cultivars both under well-watered and drought conditions. The Alba cultivar, which had the lowest OA value of the cultivars, had the highest RGR under irrigated conditions, but the high OA cultivars showed a higher RGR than the low OA cultivars under drought conditions (Degu et al., 2008). This contradicts Ayele et al.'s (2001) findings that higher OA did not result in better growth during drought. It has been noted that the widely adapted DZ-01-354 variety has a lower OA than the DZ-01-99 variety, which was bred for low water stress environments. Therefore it is possible that OA is not the only drought resistance mechanism operating in tef (Ayele et al., 2001).

Though Ayele et al. (2001) did not find any significant link between OA and root depth among tef cultivars, this could have been because the two values were measured in separate experiments. Different tef cultivars were found to have a wide variety of maximum and total root lengths, as well as a range of root length responses to drought (Ayele et al., 2001; Degu et al., 2008). The Kaye Murri and Ada varieties, which had intermediate to high OA values, showed an increase in maximum root length (MRL) under drought conditions, which could at least partially explain why these cultivars were less prone to extreme drops in leaf net assimilation (Pn) in response to drought stress (Degu et al., 2008). The Fesho variety, which had the highest OA values, however, had a decrease in MRL under drought conditions (Degu et al., 2008). This high OA is thought to be the reason why the Fesho variety maintained the highest rate of transpiration of all of the cultivars as drought stress increased (Degu et al., 2008). Later maturing cultivars, such as Kaye Murri, have deeper roots than early maturing varieties, such as Fesho (Ayele et al., 2001). The varieties with the lower OA values had a decrease in MRL under drought conditions (Degu et al., 2008). Degu et al. (2008) suggested that OA and changes in root length are separate drought responses that can occur to varying degrees across cultivars. The authors further suggested that cultivars with higher root growth might be able to access more water to avoid drought conditions, while cultivars with higher OA were better at maintaining photosynthesis and water uptake under drought conditions. Another water stress response examined in tef was leaf rolling. Cultivars with higher OA levels were found to have had fewer rolled leaves than cultivars with low OA levels (Degu et al., 2008).

Differences in the response of leaf water potential and leaf relative water content to drought were found among the different tef cultivars (Belay and Baker, 1996). Leaf water potential, leaf relative water content, transpiration rate, leaf net assimilation, and net photosynthesis in tef have all been found to decrease in response to water stress (Belay and Baker, 1996; Takele et al., 2001; Degu et al., 2008). All varieties tested by Degu et al. (2008), except for the drought resistant Kaye Murri variety, saw a larger decrease in leaf net assimilation from unstressed levels as the duration of drought conditions increased. Leaf stomatal conductance was found to be much more sensitive to stress than net photosynthesis and therefore a more sensitive indicator of stress tolerance in cultivars (Takele et al., 2001). The canopy temperature of tef has also been found to rise from 29.7 to 34.5 °C under unstressed conditions to 33.1–37.6 °C under stressed conditions (Takele, 2001).

Degu et al. (2008) measured the effects of drought on leaf net assimilation (Pn) and transpiration (E). The measurements were taken at an ambient temperature of 30 °C. There was significant variation among the different cultivars, especially under drought conditions (see Fig. 5). The mean unstressed Pn across all measured cultivars was 24.21 $\mu\text{mol}/\text{m}^2/\text{s}$ (Degu et al., 2008). The unstressed Pn measurements for the individual cultivars, however, ranged from 20.9 $\mu\text{mol}/\text{m}^2/\text{s}$ for the drought sensitive Alba variety to 26.8 $\mu\text{mol}/\text{m}^2/\text{s}$ for the also drought sensitive Balami variety (Degu et al., 2008). The more drought tolerant cultivars were closer to the mean unstressed Pn value. Transpiration did not directly correspond to Pn (Degu et al., 2008). The Alba variety,

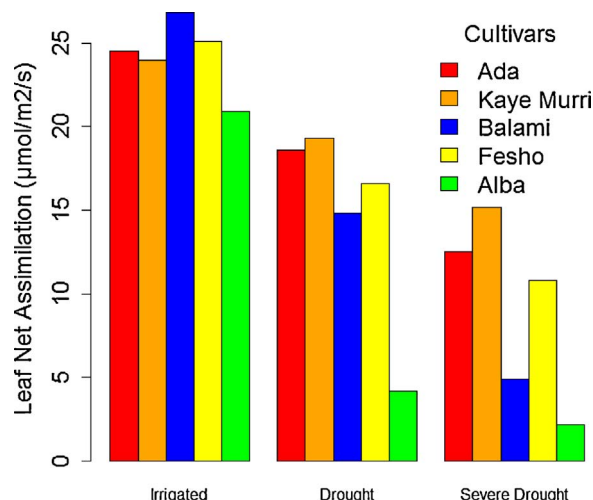


Fig. 5. Leaf net assimilation (Pn) after 24 days of irrigated, drought, and severe drought conditions at an ambient temperature of 30 °C (Degu et al., 2008).

which had the lowest unstressed Pn, had the second highest unstressed E, while the Balami variety, which had the highest unstressed Pn, had the second lowest unstressed E. There were some consistent trends, however, with the drought resistant Kaye Murri cultivar having only small decreases in both Pn and E as drought stress increased. The drought sensitive varieties Alba and Balami both saw large drops in Pn and E as drought stress increased. The Alba variety, however, appeared to have larger losses in Pn, while the Balami variety had larger losses in E as drought stress increased (Degu et al., 2008).

5.4. Crop nitrogen and grain protein

There are no studies determining the minimum N concentration of the total aboveground biomass, the biomass N concentration at emergence, or the critical tissue N concentration for the developing seed embryo for tef. There are, however, multiple studies that measured the grain and biomass N concentrations under varying N treatments (see Table 4). The control treatments that did not apply any fertilizer are the most representative of the minimum N concentration. The lowest measured plant top N concentration at maturity was 0.009 g N/g dry matter (Habtegebrail and Singh, 2006). A greenhouse experiment recorded top N concentrations as low as 0.006 under fertilized conditions, but this was using dry matter weight at grain filling stage, and not the final dry matter (Tulema et al., 2005).

Reports of grain protein content vary. Bultosa and Taylor (2004) reported the range of tef seed protein being between 9.4 and 13.3%.

The National Research Council (1996) reported the grain protein content to be between 9 and 11%. Alemayehu (1995) measured grain protein values ranging from 9.7% to 14.3%. There is limited information on how growing conditions affect the nutritional value of tef grain. Alemayehu (1995) grew twelve tef cultivars at three different locations using no fertilizer. The study converted measured grain N to grain protein by multiplying g N/100 g tef flour by 5.7, following the procedure by Tkachuk and Trvina (1969) and Tkachuk (1977). Variation in protein content among cultivars was statistically significant ($p < 0.05$) at two of the sites (Alemayehu, 1995). The variation between sites was greater than the variation between cultivars, however, indicating that the environment had a greater effect on grain protein content than genetics. While the paper noted that environmental, agronomic, and soil data were recorded for the various locations, none of this data was reported, so it is not possible to discern which environmental factors had an effect on tef protein content (Alemayehu, 1995). Zewdu and Solomon (2007) obtained the grain they tested for protein from the local market, so the effects of the environment on the protein content cannot be assessed.

There are several studies that measured the grain N content of tef under varying growing conditions, but did not report the grain protein content (Kidanu et al., 2000; Habtegebrail and Singh, 2006; Getu, 2012; Giday, 2012). Assuming the grain N to grain protein conversion factor used by Alemayehu (1995) remains constant, these studies could be used to evaluate the effect of the environment on grain protein. The calculations for the following values used g N/100 g grain, rather than g N/100 g flour as used by Alemayehu (1995), but this should have no effect on the final results. Based on these calculations, the grain protein content of tef varies from 7.1% (Habtegebrail and Singh, 2006) to 17.5% (Giday, 2012). These extreme values fall outside of the reported range of grain protein contents for tef. The average calculated grain protein value across all treatments from Getu (2012) was 15.4%, which is above the highest reported value of 14.3% (Alemayehu, 1995). At 14.5%, the average calculated grain protein value for Giday (2012) was slightly higher than the highest reported value. The average calculated grain protein values for Kidanu et al. (2000) and Habtegebrail and Singh (2006) were 12.4% and 9.8% respectively, which is within the range reported by Alemayehu (1995).

There was no clear relationship between applied fertilizer and grain protein content. Getu (2012) found that grain N, and therefore grain protein, was higher for all of the fertilized treatments than for the unfertilized control. The 23 kg N/ha treatment, however, had a higher grain N content than the 46 kg N/ha and the 69 kg N/ha treatments. Giday's (2012) results show a consistent positive relationship between applied N fertilizer and grain. Kidanu et al. (2000) showed that increasing the amount of N fertilizer applied in both the previous and the current growing season also increased the grain N content.

Table 4

N concentrations for straw and grain at crop maturity. N treatments were chosen to reflect the lowest and highest grain N concentrations.

Source	Total N Uptake (kg N/ha)		Total Biomass (Grain + Straw) Yield (kg/ha) ^a		Calculated Grain N Concentration (g N/g Grain) ^a		Calculated Straw N Concentration (g N/g Straw)		Calculated Plant Top N Concentration (g N/g dry matter)	
	Low	High	Low	High	Low	High	Low	High	Low	High
(Getu, 2012) ^b	20	41	2102	3025	0.023	0.031	0.004	0.005	0.010	0.014
(Giday, 2012) ^c	77	205.9	5455	9222	0.013	0.31	0.013	0.018	0.014	0.022
(Kidanu et al., 2000) ^d	29	87	2637	6166	0.20	0.24	0.06	0.09	0.011	0.014
(Habtegebrail and Singh, 2006) ^e	45	204	5200	6300	0.012	0.025	0.008	0.034	0.009	0.032

^a Grain is at 0% moisture.

^b Low values were from the Control (0 kg N/ha) treatment, and high values were from the 23 kg N in USG/ha treatment.

^c Low values were from the Control (0 kg N/ha) treatment, and high values were from the 69 kg N in USG/ha treatment.

^d Low values were from the 0 kg N/ha previous season & 0 kg N/ha current season treatment, and high values were from the 60 kg N/ha previous season and 60 kg N/ha current season treatment.

^e Low values were from the 0 kg N/ha and 32 kg S/ha whole application treatment in 2005, and high values were from the split application 105 kg N/ha and 0 kg S/ha treatment in 2005.

Habtegebrial and Singh's (2006) measurements showed an increase in grain N with increasing N fertilizer, except for in two cases. One of these cases saw a decrease in grain protein from 10.2% to 9.2% when the applied N fertilizer increased from 70 to 105 kg N/ha. The other case was when grain protein remained stable at 10.5% when the fertilizer was increased from 70 to 105 kg N/ha. High fertilizer application rates could result in a leveling off or decrease in grain protein due to luxury N consumption, or increased lodging.

5.5. Iron content

Reports of the iron content of tef vary. Mengesha (1966) measured grain iron levels ranging from 95 ppm to 241 ppm. Purple tef cultivars were found to have a higher iron content than white tef cultivars (Mengesha, 1966). Mamo et al. (2001) reported a grain iron content of 51 ppm for the cultivar DZ-01-354, which has white seeds, and 49 ppm for the cultivar DZ-01-99, which has brown seeds. While there have been publications that reference the iron content of tef (Mengesha, 1966; Mamo et al., 2001), there is limited information on how growing conditions affect the nutritional value of tef grain. Mamo et al. (2001) merely summarized the debate over whether, or not, tef has a higher than average iron content, and did not go into the relationship between growing conditions and grain iron content.

6. Crop management

Tef is sown at a much higher density than is common for wheat. If row planting is used, it is recommended that rows are less than 15 cm apart (Miller, 2011). In Ethiopia, tef is usually broadcast planted (Seyfu, 1997). Van Delden (2011) used a plant population density of 200 plants/m², but others used 923 plants/m² (Araya et al., 2011) and 2000 plants/m² (Tsegay et al., 2012). The recommended seeding rate for tef in Ethiopia is between 25 and 30 kg seeds/ha (Seyfu, 1997), and several studies reported using a seeding rate in this range (Kidanu et al., 2000; Habtegebrial and Singh, 2006; Oicha et al., 2010; Araya et al., 2011; Agegnehu et al., 2014). The recommended seeding rate for forage tef production in the USA is roughly 7 kg seeds/ha (Norberg et al., 2009). Araya et al. (2010) estimated their germination rate to be 70%, when they planted 24 kg seeds/ha and got approximately 1900 plants/m². The wide range in plant densities, as well as the tendency to report the seeding rate rather than the plant density, make it difficult to scale plant level measurements up to the field level and field level measurements down to a plant or leaf scale.

7. Lodging

7.1. Effects and causes

Seyfu (1993) defined three forms of permanent lodging: bend, break, and root. Bend lodging results in the plant bending without breaking or being uprooted due to loss of elasticity in the stem tissue. Break lodging results in the stem breaking, rather than bending, though the roots remain in the ground. Root lodging results in the entire plant being uprooted (Seyfu, 1993). Seyfu (1993) also defined transient lodging as a temporary form of lodging that occurs before heading due to heavy wind and, or, rains. Transient lodging is reversible due to the continued meristematic activity of the nodes (Seyfu, 1993). Van Delden (2011) divided lodging into anchorage failure, also known as root failure, and shoot failure.

Lodging is a common problem in tef production (Tekalign, 2007). Fufa et al. (1999) found that the lodging index, as defined by Caldicott and Nuttal (1979), for tef ranged from 20.0 to 99.6. Chanyalew et al. (2015) measured the lodging index for tef across various planting methods and sowing rates. The lodging indices ranged from 56.0 to 73.8 for broadcasting and from 64.5 to 76.0 for row spacing. The change in seeding rate did not have a clear correlation with the lodging

index (Chanyalew et al., 2015). Settie et al. (1996) performed a multi-year study of multiple tef varieties grown under rain fed and fertilized conditions. They found that the mean percent lodging across all years and varieties was 45% on black soils, and 40% on red soils (Settie et al., 1996). Lodging is a significant source of yield loss in tef (Seyfu, 1997; Van Delden, 2011) as it results in improper ripening, moldy panicles, subpar seed quality, and premature seed sprouting (Van Delden, 2011). Overall, Seyfu (1983) estimated that lodging resulted in grain yield losses between 11 and 22%, with an average loss of 17%. These losses are due to an estimated 35% loss in 1000-seed weight and a 51% reduction in grain yield per panicle. Seyfu (1983) also stated that lodging would affect the next generation with a 40% reduction in percent germination, and a 44% decrease in the rate of germination.

Teklu and Tefera (2005) grew multiple varieties of tef using the recommended fertilizer rates of 60 kg N/ha and 60 kg P₂O₅/ha for Vertisols and 40 kg N/ha and 60 kg P₂O₅/ha for Andosols, stringent bird control, hand weeding, and netting to prevent lodging. Under these optimal conditions, they achieved average grain yields 42% to 385% higher than those of studies that used comparable fertilizer rates, but no lodging prevention (Tulema et al., 2005; Alemayehu et al., 2006; Bedada, 2009). Clearly the yields produced by Teklu and Tefera (2005) are much higher than those achieved by experiments that did not prevent lodging using netting. While differences in soils and rainfall would also significantly affect the yields of these experiments, the evidence suggests that lodging might result in larger yield losses than the 11–22% estimated by Seyfu (1983). Teffera et al. (2000) consider lodging to be the main yield limitation for tef in areas of Ethiopia with abundant rainfall and high soil fertility.

According to Seyfu (1993), bend lodging is the most common form of lodging in tef, as well as the most economically significant form. It results in reduced grain and straw yields, makes harvesting, especially mechanized harvesting, more difficult, and promotes conditions that are favorable for the spread of pests and diseases (Seyfu, 1993). Seyfu (1993) deemed break lodging to be of only minor concern in tef production and root lodging to also be relatively insignificant. van Delden et al. (2010), however, found that tef was more susceptible to root lodging than to shoot lodging, but that poor shoot strength was also a concern.

Management practices are thought to influence the risk of lodging in tef. In particular, an abundance of nitrogen can result in excessive vegetative growth and increased lodging (Getu, 2012). Nitrogen fertilizer rates above 60 kg N/ha have been found to decrease grain yields and increase lodging (Teffera et al., 2000). Habtegebrial et al. (2007) saw up to 65% increases in lodging when the nitrogen fertilizer rate was increased from 60 kg N/ha to 90 kg N/ha. Split applications for nitrogen fertilizer are recommended in order to prevent this (Getu, 2012). The threat of increased lodging is one of the major reasons why the potential of increasing tef production by increasing fertilizer rates is limited (Seyfu, 1993). High seeding rates can also result in increased lodging, as plant crowding and competition cause weaker stems (Chanyalew et al., 2015). Early planting on lighter soils, such as Andosols, can result in more severe lodging due to faster plant establishment, increased growth rates and maturity before the cessation of the rainy season, all of which favors excessive vegetative growth (Seyfu, 1993). Tekalign (2007) found that applying a foliar spray of paclobutrazol decreased the plant height and total leaf area of tef plants, which resulted in less excessive vegetative growth and a decreased lodging percentage.

The very structure of the tef plant favors lodging. The heavy panicle makes the plant top heavy and prone to drooping (van Delden et al., 2010). As the stem grows and the panicle develops, the center of gravity of the plant shifts upwards. Norberg et al. (2009) recommended that, if tef was being grown for hay production, the plant height should be kept below 1 m and the percent heading at less than 5% in order to prevent lodging. In lodging theory, the factor of safety is used to represent how many times a support structure, such as a stem, can carry the self-

Table 5

Tef field experiments that could be used for modeling. Includes whether the paper includes the location (L), Day of Emergence (DOE), Day of Anthesis (DOA), Day of Maturity (DOM), Day of Planting (DOP), Fertilizer Application Dates (FD), Fertilizer Rates (FR), Grain Yield (GY), and Biomass Yield (BY).

Source	DOE	DOA	DOM	DOP	FD	FR	GY	BY	Notes
(Ali, 2013)			✓ ^a	✓	✓	✓	✓	✓	Yields averaged across years. USA location
(Araya et al., 2010)	✓	✓	✓	✓	✓	✓	✓	✓	Includes soil data
(Araya et al., 2011)			✓ ^b	✓ ^c	✓ ^d	✓	✓	✓	Lacks phenology data
(Balcha et al., 2006)			✓	✓	✓ ^e	✓	✓	✓	Lacks phenology data
(Bedada, 2009)	✓	✓ ^f	✓	✓		✓	✓	✓	Yields averaged over 2 locations
(Chanyalew et al., 2015)			✓				✓ ^g	✓ ^g	Lacks phenology data.
(Davison and Laca, 2010)		✓ ^h	✓ ^a	✓			✓	✓	Lacks phenology data. USA location
(Getu, 2012)		✓	✓		✓ ^e	✓	✓	✓	Lacks phenology data.
(Giday, 2012)		✓ ^f	✓			✓	✓	✓	No planting date
(Habtegebrial and Singh, 2006)				✓		✓	✓	✓	Lacks phenology data.
(Habtegebrial et al., 2007)				✓	✓	✓	✓	✓	Lacks phenology data.
(Kidanu et al., 2000)			✓ ⁱ	✓ ^c		✓	✓	✓	Lacks phenology data.
(Oicha et al., 2010)			✓	✓		✓	✓	✓	Lacks phenology data.
(Settie et al., 1996)		✓ ^f	✓ ^j	✓ ^c		✓	✓	✓ ^g	Lacks phenology data.
(Tekalign, 2007)			✓			✓	✓	✓	No planting date.
(Teklu and Tefera, 2005)		✓ ^f	✓			✓	✓	✓	No planting date.
(Tsegay et al., 2012)	✓	✓	✓	✓	✓ ^e	✓	✓ ^k		Unclear yield data
(Tsegay et al., 2015)				✓			✓		No anthesis or maturity dates.
(Tulema et al., 2007)			✓ ^a	✓	✓	✓	✓	✓	No anthesis date
(Tulema et al., 2008)			✓ ^a	✓		✓ ⁱ	✓	✓	Lacks phenology data.
(Tulema et al., 2005)			✓ ^a	✓		✓ ⁱ	✓	✓	Missing anthesis date.

^a Reported the harvest date, not the physiological maturity date. Tef is normally harvested close to maturity.

^b Reported the length of the growing period (days).

^c Only provided a rough planting time frame, not a specific planting date.

^d Fertilizer application times were reported in relation to sowing, and not as a specific date.

^e Fertilizer application times were reported in terms of growth stage, and not a specific date.

^f Reported days to heading, not the anthesis date.

^g Yield was averaged across multiple years.

^h Reported the date of heading, not the anthesis date.

ⁱ Reported that harvest was in September. Did not report a specific maturity date.

^j Reported days to maturity, not the specific date of maturity.

^k Yields were reported in a graph that did not specify which yield corresponded to which treatment.

^l Reportedly used the national average rate, but it is unclear what this rate is.

weight moment of the structure it bears, such as a spike (Crook et al., 1994). The whole plant self-weight moment (M_p) is calculated by:

$$M_p = \sin \theta \times h_p \times m_p \times g \quad (1)$$

Where θ is the angle in degrees from the vertical, h_p is the height in m of the center of gravity of the plant, m_p is the mass of the plant in kg, and g is the acceleration due to gravity (m/s^2) (Crook et al., 1994). The unit of M_p is Newton-meters (N-m) (Crook et al., 1994). On sandy soils, lodging was found to be inevitable due to the plant reaching the critical safety factor against anchorage failure well before the maximum M_p is reached (van Delden et al., 2010). The same experiment also found that tef had poor anchorage strength, possibly due to flexible vertical roots and a shallow crown depth. Shallow roots and weak shoots both were found to contribute to lodging in tef. The bending strength, the maximum self-weight moment that the base of the shoot can support before it fails, and flexural rigidity, the Young's Modulus multiplied by the second moment of area, of tef were found to be much lower than that of wheat and rice. Tef had a bending strength varying between 0.02 and 0.07 N-m depending on the variety (van Delden et al., 2010), while winter wheat had 0.16 N-m (Crook and Ennos, 1993; Crook et al., 1994) and rice had 2.5 N-m (Chuanren et al., 2004; Oladokun and Ennos, 2006). The flexural rigidity of tef was between 0.002 and 0.01 N-m², depending on the cultivar (van Delden et al., 2010). The flexural rigidity of wheat is estimated to be 0.04 N-m² (Crook and Ennos, 1993; Crook et al., 1994) and that of rice to be 1.8 N-m² (Chuanren et al., 2004; Oladokun and Ennos, 2006). The shoot diameter of tef, which varied between 1.8 and 3.2 mm depending on the variety (van Delden et al., 2010), was also smaller than that of wheat and rice, which are reported as 4.5 mm (Crook and Ennos, 1993; Crook et al., 1994) and 6.6 mm (Chuanren et al., 2004; Oladokun and Ennos, 2006) respectively. The Young's Modulus of tef, however, was found to be higher

than that of wheat. Based on their findings, van Delden et al. (2010) suggested that increased stem diameter and enhanced root anchorage would be the most effective traits to breed for, in order to decrease lodging. Seyfu (1993) noted several characteristics that improve lodging resistance in tef without compromising grain yield. These included a culm thickness between 2.5 and 3.1 mm, a panicle length of 47 cm or less, a peduncle that is 10 cm long or less, a culm length less than or equal to 60 cm, a peduncle to panicle length ratio between 0.2 and 0.3, and a panicle to culm length ratio between 0.7–1.0 (Seyfu, 1993).

7.2. Lodging model

There are multiple biomechanical models for assessing lodging in individual plants. Crook et al. (1994) developed a biomechanical lodging model for cereals that was based on the behavior of wheat, which has an erect spike. Unlike wheat, the drooping tef panicle has a non-zero self-weight moment, which goes against one of the assumptions of the Crook et al. (1994) model. The model also assumes that the behavior of the shoots is comparable to that of a uniform rigid beam (Crook et al., 1994), which is inconsistent with tef's tapering shoots and tendency to bend under its own weight (van Delden et al., 2010). Because of the shortcomings of the Crook et al. (1994) model for tef, van Delden et al. (2010) proposed corrections to the model, including a suggestion to include the effects that the added weight, caused by a wet panicle, would have on the biomechanics of the plant. As crop models do not generally focus on individual plants, however, neither of these models are likely to be used to simulate lodging on a larger scale.

8. Field data availability

8.1. Available field experiments

Model development requires accurate and well documented field data. The less uncertainty there is in the input data, the more easily one can locate sources of error in the model. Table 5 lists field experiments that are possible candidates for model development. This list does not include pot or greenhouse experiments, as these usually do not represent field conditions.

8.2. Research gaps

For many tef field experiments, planting dates are not reported (Teklu and Tefera, 2005; Rockstrom et al., 2009; Giday, 2012), or only roughly estimated (Kidanu et al., 2000; Habtegebrial et al., 2007; Araya et al., 2011; Agegnehu et al., 2014). Most studies list the time to heading (Seyfu, 1993; Settie et al., 1996; Ayele et al., 2001; Tadesse, 2005; Teklu and Tefera, 2005; Bedada, 2009; Davison and Laca, 2010; Van Delden, 2011; Giday, 2012) rather than the time to anthesis (Araya et al., 2010; Getu, 2012; Tsegay et al., 2012). The temperature for maximum thermal time accumulation for phenology is unknown. It is also unknown if the effect of temperature on thermal time accumulation varies between the vegetative and reproductive stage, as it does for sorghum, and what the maximum temperature is for thermal time accumulation. Further research is needed on the canopy level radiation use efficiency of tef, the effect that temperature has on radiation use efficiency, the leaf area index, and the light extinction coefficient. Much of the data available on photosynthesis was measured on the leaf level (Kebede et al., 1989; Degu et al., 2008), and not the canopy level at which most models operate. RUE could possibly be estimated from existing canopy cover and aboveground biomass time series data (Araya et al., 2010), but this data is limited and only satellite radiation data is available. More information is also needed on the early stages of growth, including the effects of soil moisture on germination and biomass N concentration at emergence.

Complete environmental and management data is rarely reported for tef field experiments, which will result in the modeler having to make assumptions for some of the model inputs listed in Fig. 2. Daily weather data are almost never reported in tef experiments (Haileselassie et al., 2016), and publications usually only include monthly rainfall totals (Kidanu et al., 2000; Tulema et al., 2005; Habtegebrial and Singh, 2006; Habtegebrial et al., 2007; Tulema et al., 2008), or average minimum and maximum temperatures for the entire growing season (Balcha et al., 2006; Getu, 2012). The Ethiopian National Meteorology Agency (NMA) does maintain a network of weather stations, but many of the weather records are not digitized and therefore not readily accessible (NMA, 2017). Satellite data is available from the NASA Prediction of Worldwide Energy Resource (POWER) service, but rainfall data are only available from 1997 onwards, and the weather data is an average across a 1° latitude by 1° longitude grid, which means that it is not accurate for localized phenomena such as rainfall (NASA, 2017). Another source of satellite weather data is the Climate Hazards Group InfraRed Precipitation with Station (CHIRPS) data set, which goes back to 1981 and has a 0.05° resolution (Funk et al., 2015). Only two of the studies examined for this paper reported both the water holding properties and the nutrient content of the soil (Habtegebrial et al., 2007; Haileselassie et al., 2016). In the case of split fertilizer applications, the timing of the second application is often reported in terms of the developmental stage, such as early tillering, and not in terms of days after planting (Teklu and Tefera, 2005; Balcha et al., 2006; Habtegebrial and Singh, 2006; Tsegay et al., 2012; Agegnehu et al., 2014). The developmental rate of tef varies greatly between cultivars (Seyfu, 1997), making it difficult to estimate how many days after planting a certain developmental stage may be. Field experiments comparing phenological stages in different growing environments (e.g.

via a range of sowing dates or at different locations) across tef cultivars would be useful to quantify parameters for tef phenology model routines.

In order to adapt a tef model to outside of Ethiopia, more field trials are needed at higher latitudes. Many of the agronomic tef experiments outside of Ethiopia are greenhouse experiments (Ayele et al., 2001; Tulema et al., 2005; Degu et al., 2008; Ghebrehewot et al., 2008; Evert et al., 2009; Van Delden, 2011), and thus difficult to relate to a field scale model. Elevated CO₂ trials for tef would provide a better understanding of the effects of climate change on tef than simply using the results from other C4 crops. The effects of heat stress on tef phenology and growth require further investigation, to understand both how tef would fare in hotter climates, and how climate change in Ethiopia or elsewhere would affect tef. Further research on the causes of lodging and the development of a field level lodging model are also needed.

9. Conclusions

Tef plays an important role in Ethiopian food security. Creating a comprehensive crop model for tef would allow for a better understanding of tef production under varying environmental conditions and management approaches. Important data to have when creating a crop model include phenology, radiation use efficiency, CO₂ effects, nitrogen responses, water responses, and temperature stress responses. Tef's tendency towards lodging suggests that the inclusion of a lodging routine is also important. Not all of this data is available for tef, but estimates for missing data might be inferred from other cereal crops. Using a combination of tef and cereal literature, it should be possible to develop a crop model prototype for tef, though further research is still needed.

Conflicts of interest

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